# SURVEY OF SOCIAL INSECTS
# IN THE FOSSIL RECORD*

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Biologists have long been intrigued by the complex social systems of various insects. Despite a voluminous literature dealing with the evolution of these systems, immense gaps remain in our understanding of insect sociality. Several theories have been proposed to explain the evolution of social behavior in certain groups of insects (e.g., Hamilton, 1964), but none consider this problem with respect to geological time. The present paper does so by examining the fossil record for clues not only on the antiquity of sociality, but also on the nature of these early social insects. Included in this survey are those insects recognized as eusocial: the Isoptera, and three superfamilies of the Hymenoptera: Vespoidea, Formicoidea, and Apoidea.

## ISOPTERA

The termites are remarkable in two regards: 1) as a group, they are fully eusocial, exhibiting a wide range of behavioral modifications and sophistications, and 2) their record in the geological past, although sparse, is highly indicative of an Early Mesozoic origin. This latter point is of particular significance if one considers sociality among insects as a pinnacle of evolutionary success. Wilson (1971, p. 1) states that "[insect societies] best exemplify the full sweep of ascending levels of organization, from molecule to society." The possibility that termites evolved a social organization as far back in geological time as the Jurassic (roughly 190 million years ago) is of great interest, particularly when attempting to draw parallels with the evolution of sociality in the Hymenoptera, a group phylogenetically very remote from the termites.

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Five of the six families[1] of termites recognized by Emerson (1955) have a fossil record extending at least as far back as the Tertiary. In 1967, *Cretatermes carpenteri* (Hodotermitidae) was found in an Upper Cretaceous deposit in Labrador (Fig. 1), a discovery which immediately placed the origin of the Isoptera no later than the Mesozoic — an extension of 45 million years from previously known specimens. In addition, the advanced phylogenetic position of *Cretatermes* provides evidence for a much earlier origin of the order than has formerly been recognized (Emerson, 1967).

An examination of various fossil localities reveals a widespread termite fauna during the Tertiary Period (Table 1). The Termitidae are found in Miocene deposits of California and Germany; the Rhinotermitidae, Hodotermitidae, and Kalotermitidae are found at various Tertiary deposits throughout the United States and Europe; and the Mastotermitidae have the most widespread Cenozoic distribution of all, having been found at localities in the United States, Europe, South America, and Australia. This latter finding is highly intriguing because the family Mastotermitidae today has but one species, *Mastotermes darwiniensis,* which is restricted to northern Australia.[2] Emerson (1955) postulates that this widespread

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[1]The sixth family is the Serritermitidae — an aberrant taxon known from only one species.

[2]A look at past climatic shifts provides additional insight into the redistribution of the termites, particularly with respect to the Mastotermitidae, now solely restricted to Australia. Reconstructions of paleo-climatic patterns may be made fairly accurately on the basis of floral analyses (Reid and Chandler, 1933). The presence of *Sequoia* stumps in the Florissant Shales of Colorado provides evidence for warmer temperatures during the Oligocene (Emerson, 1969). Tiffney (1977) postulates on the basis of fossil angiosperm assemblages that temperatures in New England during the Oligocene were much more equable than at present — the temperatures ranging from 26° C to 9° C in contrast to today's 21° C to −10° C. Furthermore, extended frosts and hard freezes were unknown. In the more tropical climate of the Oligocene, colony activities were presumably carried out year round in a relatively warm, moist environment, explaining the widespread distribution of the Mastotermitidae during the Lower to Middle Tertiary. By the Late Miocene or Early Pliocene, the earth's climate began shifting towards cooler temperatures with the rising level of the continental land masses and increasingly large polar ice caps. My hypothesis is that, unable to adapt to an increasingly colder climate, and possibly to a concomitant change in predator pressures, the Mastotermitidae began to die out during the Tertiary. And, because at this time the Termitidae were undergoing tremendously successful radiation in Africa and South America, the Mastotermitidae became geographically restricted to northern Australia, represented today by only one relict species, *Mastotermes darwiniensis.*

Figure 1. *Cretatermes carpenteri* Emerson from lower part of Upper Cretaceous of Labrador. Note humeral suture at wing base. Original photograph of holotype in Princeton Museum. Length of wing, 7.5 mm.

geographical distribution provides strong evidence to support a Mesozoic origin of the order. He argues (1975) that the breakup of the united land mass Pangaea in the Permian or Lower Triassic must have occurred subsequently to the origin of the Isoptera to explain their distribution in the southern and northern continental land masses and that all five families must have been present in the Late Mesozoic to explain their diversity and distribution by the Tertiary.

In 1971 he looked at a variety of primitive and derived characters of each family and analyzed the geographical distribution of the groups, using plate tectonics to provide the following estimates on the geological origin of the families:

Mastotermitidae — possibly Early Mesozoic.

Hodotermitidae — Triassic, or Early Jurassic before the breakup of southern continents.

Kalotermitidae — mid-Jurassic, or Lower Cretaceous, before the separation of Africa and South America.

Rhinotermitidae — Late Jurassic, Early Cretaceous.

Termitidae — Cretaceous.

Because termites are such poor fliers and do not mate until the adults have cast their wings, he considers water gaps of more than 50 miles capable of preventing termite dispersal.

While I am supportive of the theory that places great importance on the role of a unified land mass in animal dispersal, I do not agree that this can effectively be used to date the origin of the Isoptera.

TABLE 1　ISOPTERA IN THE FOSSIL RECORD.

| Geological Age | Locality | References |
|---|---|---|
| CRETACEOUS | | |
| Hodotermitidae | | |
| *Cretatermes carpenteri* Emerson | Labrador, Canada | Emerson, 1967 |
| EOCENE | | |
| Mastotermitidae | | |
| *Blattotermes wheeleri* Collins | Tennessee, U.S.A. | Emerson, 1965 |
| *Idomastotermes mysticus* Häupt | Geiseltal, Germany | Emerson, 1965 |
| Kalotermitidae | | |
| *Neotermes grassei* Piton | Menat, France | Emerson, 1969 |
| Hodotermitidae | | |
| *Termopsis mallaszi* Pongracz | Hungary | Snyder, 1949 |
| OLIGOCENE | | |
| Mastotermitidae | | |
| *Miotermes insignis* (Heer) | Oeningen, Germany | Emerson, 1965 |
| *Miotermes spectabilis* (Heer) | Oeningen, Germany | Emerson, 1965 |
| *Mastotermes bournemouthensis* von Rosen | England | Emerson, 1965 |
| *Mastotermes heeri* (Göppert) | Schlesien, Germany | Emerson, 1965 |
| *Mastotermes batheri* von Rosen | England | Emerson, 1965 |
| Kalotermitidae | | |
| *Prokalotermes hageni* (Scudder) | Florissant, Colorado | Emerson, 1969 |
| *Electrotermes giradi* (Giebel) | Baltic Amber | Emerson, 1969 |
| *Electrotermes affinis* (Hagen) | Baltic Amber | Emerson, 1969 |
| *Kalotermes rhenanus* Hagen | Rott, Germany | Emerson, 1969 |
| *Eotermes grandaeva* Statz | Rott, Germany | Emerson, 1969 |
| *Proelectrotermes berendtii* (Pictet) | Baltic Amber | Emerson, 1969 |

Hodotermitidae

| | | |
|---|---|---|
| *Archotermopsis tornquisti* von Rosen | Baltic Amber | Snyder, 1949 |
| *Termopsis bremii* Heer | Baltic Amber | Snyder, 1949 |
| *Parotermes insignis* Scudder | Florissant, Colorado | Snyder, 1949 |
| *Parotermes scudderi* Cockerell | Florissant, Colorado | Cockerell, 1913 |
| *Ulmeriella bauckhorni* Meunier | Rott, Germany | Emerson, 1968 |
| *Ulmeriella cockerelli* Martynov | Siberia, U.S.S.R. | Emerson, 1968 |

Rhinotermitidae

| | | |
|---|---|---|
| *Reticulitermes minimus* (Snyder) | Baltic Amber | Emerson, 1971 |
| *Reticulitermes fossarum* (Scudder) | Florissant, Colorado | Emerson, 1971 |
| *Reticulitermes antiquus* (Germar) | Baltic Amber | Emerson, 1971 |
| *Reticulitermes creedei* Snyder | Creede, Colorado | Emerson, 1971 |
| *Parastylotermes robustus* (Rosen) | Baltic Amber | Emerson, 1971 |

MIOCENE

Mastotermitidae

| | | |
|---|---|---|
| *Spargotermes costalimai* Emerson | Brazil | Emerson, 1965 |
| *Mastotermes vetustus* Pongracz | Radoboj, Croatia | Emerson, 1965 |
| *Mastotermes minor* Pongracz | Radoboj, Croatia | Emerson, 1965 |
| *Mastotermes haidingeri* (Heer) | Radoboj, Croatia | Emerson, 1965 |
| *Mastotermes croaticus* von Rosen | Radoboj, Croatia | Emerson, 1965 |
| *Miotermes procerus* (Heer) | Radoboj, Croatia | Emerson, 1965 |
| *Miotermes randeckenensis* von Rosen | Württemberg, Germany | Emerson, 1965 |
| *Pliotermes hungaricus* Pongracz | Radoboj, Croatia | Emerson, 1965 |

Kalotermitidae

| | | |
|---|---|---|
| *Cryptotermes ryshkoffi* Pierce | Calico, California | Emerson, 1969 |
| *Kalotermes swinhoei* (Cockerell) | Burma | Emerson, 1969 |
| *Kalotermes tristis* (Cockerell) | Burma | Emerson, 1969 |
| *Kalotermes nigritus* Snyder | Chiapas, Mexico | Snyder, 1960 |

# TABLE 1  ISOPTERA IN THE FOSSIL RECORD

| Geological Age | Locality | References |
|---|---|---|
| **CRETACEOUS** | | |
| Hodotermitidae | | |
| •*Cretatermes carpenteri* Emerson | Labrador, Canada | Emerson, 1967 |
| **EOCENE** | | |
| Mastotermitidae | | |
| •*Blattotermes wheeleri* \|Collins | Tennessee, U.S.A | Emerson, 1965 |
| •*Idomastotermes mysticus* Haupt | Geiseltal, Germany | Emerson, 1965 |
| Kalotermitidae | | |
| *Neotermes grassei* Piton | Menat, France | Emerson, 1969 |
| Hodotermitidae | | |
| *Termopsis mallaszi* Pongracz | Hungary | Snyder, 1949 |
| **OLIGOCENE** | | |
| Mastotermitidae | | |
| •*Miotermes insignis* (Heer) | Oeningen, Germany | Emerson, 1965 |
| •*Miotermes spectabilis* (Heer) | Oeningen, Germany | Emerson, 1965 |
| *Mastotermes bournemouthensis* von Rosen | England | Emerson, 1965 |
| *Mastotermes heeri* (Göppert) | Schlesien, Germany | Emerson, 1965 |
| *Mastotermes batheri* von Rosen | England | Emerson, 1965 |
| Kalotermitidae | | |
| •*Prokalotermes hageni* (Scudder) | Florissant, Colorado | Emerson, 1969 |
| •*Electrotermes giradi* (Giebel) | Baltic Amber | Emerson, 1969 |
| •*Electrotermes affinis* (Hagen) | Baltic Amber | Emerson, 1969 |
| *Kalotermes rhenanus* Hagen | Rott, Germany | Emerson, 1969 |
| •*Eotermes grandaeva* Statz | Rott, Germany | Emerson, 1969 |
| •*Proelectrotermes berendti* (Pictet) | Baltic Amber | Emerson, 1969 |

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| | | |
|---|---|---|
| Hodotermitidae | | |
| *Archotermopsis tornquisti* von Rosen | Baltic Amber | Snyder, 1949 |
| *Termopsis brenii* Heer | Baltic Amber | Snyder, 1949 |
| •*Parotermes insignis* Scudder | Florissant, Colorado | Snyder, 1949 |
| •*Parotermes scudderi* Cockerell | Florissant, Colorado | Cockerell, 1913 |
| •*Ulmeriella bauckhorni* Meunier | Rott, Germany | Emerson, 1968 |
| •*Ulmeriella cockerelli* Martynov | Siberia, U.S.S.R. | Emerson, 1968 |
| Rhinotermitidae | | |
| •*Reticulitermes minimus* (Snyder) | Baltic Amber | Emerson, 1971 |
| *Reticulitermes fossarum* (Scudder) | Florissant, Colorado | Emerson, 1971 |
| *Reticulitermes antiquus* (Germar) | Baltic Amber | Emerson, 1971 |
| *Reticulitermes creedei* Snyder | Creede, Colorado | Emerson, 1971 |
| •*Parastylotermes robustus* (Rosen) | Baltic Amber | Emerson, 1971 |
| **MIOCENE** | | |
| Mastotermitidae | | |
| •*Spargotermes costalimai* Emerson | Brazil | Emerson, 1965 |
| *Mastotermes vetustus* Pongracz | Radoboj, Croatia | Emerson, 1965 |
| *Mastotermes minor* Pongracz | Radoboj, Croatia | Emerson, 1965 |
| *Mastotermes haidingeri* (Heer) | Radoboj, Croatia | Emerson, 1965 |
| *Mastotermes croaticus* von Rosen | Radoboj, Croatia | Emerson, 1965 |
| •*Miotermes procerus* (Heer) | Radoboj, Croatia | Emerson, 1965 |
| •*Miotermes randeckenensis* von Rosen | Württemberg, Germany | Emerson, 1965 |
| •*Pluotermes hungaricus* Pongracz | Radoboj, Croatia | Emerson, 1965 |
| Kalotermitidae | | |
| *Cryptotermes ryshkoffi* Pierce | Calico, California | Emerson, 1969 |
| *Kalotermes swinhoei* (Cockerell) | Burma | Emerson, 1969 |
| *Kalotermes tristis* (Cockerell) | Burma | Emerson, 1969 |
| *Kalotermes nigritus* Snyder | Chiapas, Mexico | Snyder, 1960 |

TABLE 1. (CONCLUDED)

| Geological Age | Locality | References |
| --- | --- | --- |
| MIOCENE (continued) | | |
| Hodotermitidae | | |
| *Ulmeriella latahensis* Snyder | Latah, Washington | Emerson, 1968 |
| *Ulmeriella martynovi* Zeuner | Biebrich, Germany | Emerson, 1968 |
| Rhinotermitidae | | |
| *Heterotermes primaevus* Snyder | Chiapas, Mexico | Emerson, 1971 |
| *Reticulitermes hartungi* (Heer) | Radoboj, Croatia | Emerson, 1971 |
| *Reticulitermes laurae* Pierce | Calico, California | Emerson, 1971 |
| *Parastylotermes calico* Pierce | Calico, California | Emerson, 1971 |
| *Parastylotermes washingtonensis* (Snyder) | Latah, Washington | Emerson, 1971 |
| Termitidae | | |
| *Gnathamitermes magnoculus rousei* Pierce | Calico, California | Pierce, 1958 |
| *Macrotermes pristinus* (Charpentier) | Radoboj, Croatia | Snyder, 1949 |

*Extinct genera.

Simpson (1952) has made some insightful remarks on the matter. He contests the premise that if a given group of organisms requires a land connection, then disjunctive areas occupied by the group must have been once connected by continuous land. His contention is that there is no group of organisms that cannot be dispersed over water. Given a probability of only one chance in a million that an organism can cross a stretch of water, when geological time is considered the chance that the event will actually take place (over tens of millions of years) becomes significantly greater. It is further argued that successful colonization is dependent on successful invasion and the ability of the intruder to compete with existing species. Chances for survival are much higher when there are numerous, simultaneous arrivals of individuals.

In my opinion, the termites support such reasoning, and this can be argued in several ways. Firstly, termites are relatively light-bodied, winged insects. Studies by Simberloff and Wilson (1969) and Glick (1933) on the repopulation of an island by wind trans-ported insects strongly support the possibility that termites are capable of being carried considerable distances in the upper atmos-phere. Furthermore, because termites swarm in such large numbers prior to reproduction, a reasonable possibility exists that they will be dispersed to a new habitat as either a group or at least as a male/female pair. A wind current strong enough to blow one individual into the upper atmosphere should be equally capable of carrying multiple individuals, and, according to windflow, of trans-porting them in the same directional pathway.

Secondly, termites are ideally suited to dispersal over large bodies of water via floating logs. The more primitive families construct their extensive nesting colonies in wood and logs; as a consequence, it is entirely plausible that a dead tree falling into a body of circulating water could be carried extended distances. Furthermore, this mode of transportation provides the termites with a source of food during their sojourn, and travel *en masse* obviates the prob-lems of reproduction upon arrival. In addition, as Simpson points out, the larger the number of individuals, the more likely it is that they will be successful competitors in the new habitat. I am not presenting this as evidence that the termites did not evolve while the earth's land masses were still contiguous, but am merely pointing out the problems in arguing that land dispersal was essential for termites.

The Isoptera exhibit strong affinities to the Blattodea; evidence linking the two groups to a common ancestor is well marked between the Mastotermitidae, an archaic termite family, and the Cryptocercidae, a family of generalized cockroaches. This theory of common ancestry is supported by several comparative morphological and behavioral studies (Emerson, 1965; McKittrick, 1965; Ahmad, 1950; Cleveland, 1934; Hill, 1925). McKittrick (1965) goes so far as to incorporate both groups into the Dictyoptera, an order which also includes the Mantodea. The gut fauna, female genitalic structures, anal expansion of the hind wing, morphology of the proventriculus, and deposition of eggs in ootheca-like masses are much alike in *Mastotermes* and *Cryptocercus*. Furthermore, both groups inhabit similar habitats. As a consequence, termites have often been referred to as merely social cockroaches. This degree of relatedness becomes immediately interesting in view of the extensive geological record of the cockroaches.

Fossil cockroaches are first found in deposits from the Upper Carboniferous, which makes them among the oldest insects known. Furthermore, they comprise 80 percent of the fossil insect fauna during that period (Carpenter, 1930) — an indication that they have not only existed, but have flourished, for three hundred million years. If the similarities between termites and cockroaches are indeed the result of monophyletic, rather than convergent or parallel evolution, one might speculate on a much earlier origin for the Isoptera than is shown by the fossil record.

McKittrick (1965) admits that the flagellate gut fauna essential for cellulose digestion in both groups may have arisen independently in each; however, she believes that the similarities in two important morphological characters, the female genitalia and the dental belt of the proventriculus, represent primitive characters and are therefore indicative of a common origin for *Mastotermes* and *Cryptocercus*. On the other hand, Tillyard (1926, 1936), Cleveland (1934), Imms (1919), Carpenter (personal communication), among others, believe that the termites were derived from more ancient stock and may have evolved during the Late Paleozoic. Hamilton (1978) supports the view that social termites arose from "roach-like ancestors" in the habitat of dead phloem, and suggests that the invasion of *Cryptocercus* into the same type of habitat was independent of the ancestral termite. The possibility of termite "evolu-

tion under bark" seems immensely feasible; not only is isolation (and, hence, inbreeding) possible, but selective pressures leading to dependence on a cellulose diet would also be high. It seems an excellent explanation for the early separation of the termites and cockroaches from a common protorthopteran (protoblattoid) ancestor as long ago as the Late Paleozoic. More definite conclusions on the origin of the Isoptera must wait until termites or termite-like insects have been found in pre-Cretaceous strata.

## HYMENOPTERA

The Hymenoptera belong to the major subdivision of the Insecta known as the Endopterygota. There are no clues elucidating the nature or precise age of the earliest endopterygote insects, but the fossil record does provide insight into the history of the group as a whole. Representatives of two endopterygote orders, Neuroptera and Mecoptera, are found as far back as the Early Permian, some 280 million years ago. This occurrence suggests an origin of the Endopterygota approximately 100 million years after the origin of the true insects.[3]

The earliest known Hymenoptera have been found in Triassic beds of Central Asia (Rasnitsyn, 1964) and Australia (Riek, 1955). These fossils establish a minimum age for the order of about 220 million years. All the specimens known from this period belong to the suborder Symphyta, and surprisingly enough belong to the existing family Xyelidae.

A major advance in the evolution of the Hymenoptera occurred with the development of a constriction between the first and second abdominal segments; this presumably had the selective advantage of increasing the flexibility of the abdomen, important for both oviposition and defense. Hymenoptera which possess this adaptation, a diagnostic character of the suborder Apocrita, are first known from Upper Jurassic deposits of Central Asia (Rasnitsyn, 1975, 1977). These specimens have been assigned to the more primitive division of the Apocrita known as the Terebrantia or

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[3]The oldest known insects, found in Upper Carboniferous deposits, comprise 11 orders and include the Apterygota (Thysanura), Paleoptera and Exopterygota. It should be noted that here the use of the term insect does not include the Collembola, Protura or Diplura.
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Parasitica; the other division within this suborder is the Aculeata.[4]
Members of the latter are characterized by modifications of the
ovipositor that have enabled its use not only for oviposition, but
also as a transport vessel for defensive and prey-paralyzing com-
pounds. This structure unquestionably plays an important role in
colony defense and might provide an explanation for the restriction
of eusociality within the Hymenoptera to the Aculeata.

The oldest known aculeate hymenopteron, *Cretavus sibericus,* was
discovered in an Upper Cretaceous (Cenomanian) deposit in Siberia
in 1957. Although placed by Sharov (1962) in an extinct superfamily
Cretavidea, related to the Scolioidea, it has recently been transferred
to the existing family Mutillidae by Rasnitsyn (1977, p. 109). Since
1967, species representing 10 families and 19 genera of aculeate
Hymenoptera have been found in Upper Cretaceous deposits in
Central Asia (Rasnitsyn, 1977) (Table 2). Evans (1966) believes that
such diversity by the Late Cretaceous is indicative of an earlier origin
and postulates that the group may have evolved during the Jurassic.
However, it must be pointed out that the Cretaceous is one of the
longer periods in the earth's history, having a duration of roughly 70
million years, and may have been of sufficient length to account for
such diversification.

## VESPOIDEA

Included in this group are the three families considered to be "true
wasps": The Masaridae and Eumenidae, both of which are solitary,
and the Vespidae, where one finds behavioral modifications ranging
from subsocial to highly advanced eusocial (Richards, 1953, 1971).
It is the Vespidae, by virtue of their sociality, with which I am
primarily concerned in this paper.

There are many gaps in our record of the early social wasps and of
the Vespoidea in general. Most striking, perhaps, about the fossil
record of the wasps is their lack of representation (see Table 3). The

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[4]The classification of the Aculeata has recently undergone a major revision by D. J.
Brothers (1975), in which the seven previously recognized superfamilies (Bethyloidea,
Scolioidea, Pompiloidea, Formicoidea, Vespoidea, Sphecoidea, and Apoidea) are
now combined into three: the Bethyloidea, Sphecoidea (subdivided into the Spheci-
formes and Apiformes), and Vespoidea (subdivided into the Vespiformes and
Formiciformes). However, since this revised classification has not been generally
accepted in its entirety, I am employing here the more conventional classification
(*sensu* Riek, 1970; Richards, 1971).

Table 2.   Genera of aculeate Hymenoptera known from Cretaceous deposits (based on Rasnitsyn, 1977, and Evans, 1973). All genera are extinct.

SCOLIOIDEA
  Mutillidae                    *Cretavus*          Sharov, 1962;
                                                    Rasnitsyn, 1977

?SCOLIOIDEA
  Scolioidae                    *Oryctopterus*      Rasnitsyn, 1977
  Angarosphecidae               *Angarosphex*       Rasnitsyn, 1977
  Falsiformicidae               *Falsiformica*      Rasnitsyn, 1977

?SCOLIOIDEA-BETHYLOIDEA
  ?Scolebythidae                *Cretabythus*       Evans, 1973

BETHYLOIDEA
  Bethylidae                    *Archaepyris*       Evans, 1973
                                *Celonophamia*      Evans, 1973

  Cleptidae                     *Procleptes*        Evans, 1969
                                *Hypocleptes*     . Evans, 1973
                                *Protamisega*       Evans, 1973

  Dryinidae                     *Cretodryinus*      Rasnitsyn, 1977

POMPILOIDEA
  Pompilidae                    *Pompilopterus*     Rasnitsyn, 1977

FORMICOIDEA
  Formicidae                    *Sphecomyrma*       Wilson and Brown, 1967
                                *Cretomyrma*        Rasnitsyn, 1977
                                *Paleomyrmex*       Rasnitsyn, 1977

SPHECOIDEA
  Sphecidae                     *Lisponema*         Evans, 1969
                                *Pittoecus*         Evans, 1973

?SPHECOIDEA
  ?Sphecidae                    *Archisphex*        Evans, 1969
                                *Taimyrisphex*      Evans, 1973

VESPOIDEA
  Masaridae                     *Curiovespa*        Rasnitsyn, 1975

absence of Vespidae from Baltic Amber (Lower Oligocene) and other fossil resins, in which ants are abundant, is probably due to their relatively large size, which reduces the likelihood of their entrapment in the sticky tree resin. Spradbery (1973, p. 316), attributes their scarcity in sedimentary deposits to "the behavioral characteristics and paper nest structures which do not lend themselves to fossilization." As with any other fossil, the absence of an insect in the paleontological record provides no proof as to its actual occurrence in the past; one can only reconstruct and evaluate paleofaunas on the basis of those organisms that are represented. Therefore, it is conceivable that wasps were present earlier than the record indicates, but that conditions conducive to their preservation were lacking. The following does, however, provide information on the diversity of the group as we know it.

*Cretaceous*

The earliest record of the Vespoidea extends back to the Upper Cretaceous (Turonian). Two species of vespoid wasp have been found in a deposit of this age in the USSR — both assigned to the genus *Curiovespa* (Rasnitsyn, 1975). Unfortunately, nothing is known about the body structure of these insects but on the basis of their wing venation they are placed in the family Masaridae. The presence of two distinct species in the same deposit suggests that some diversification of the Vespoidea had taken place as early as the Upper Cretaceous, although nothing is known about the morphological character of these early wasps.

*Paleocene*

No Vespoidea from this period are known.

*Eocene*

The Eocene beds of Green River have yielded a surprisingly diverse assemblage of aculeates, but most of these belong to the Terebrantia or Sphecoidea; the only vespoid recovered from this deposit, *Didineis solidescens,* is of uncertain systematic position (Evans, 1966, p. 393). Scudder (1890) described this specimen as a sphecid of the subfamily Nyssoninae. However, Evans (1966) examined the type and concluded that it did not belong to the family Sphecidae, but was probably a eumenid, and tentatively assigned it to the genus *Alastor.*
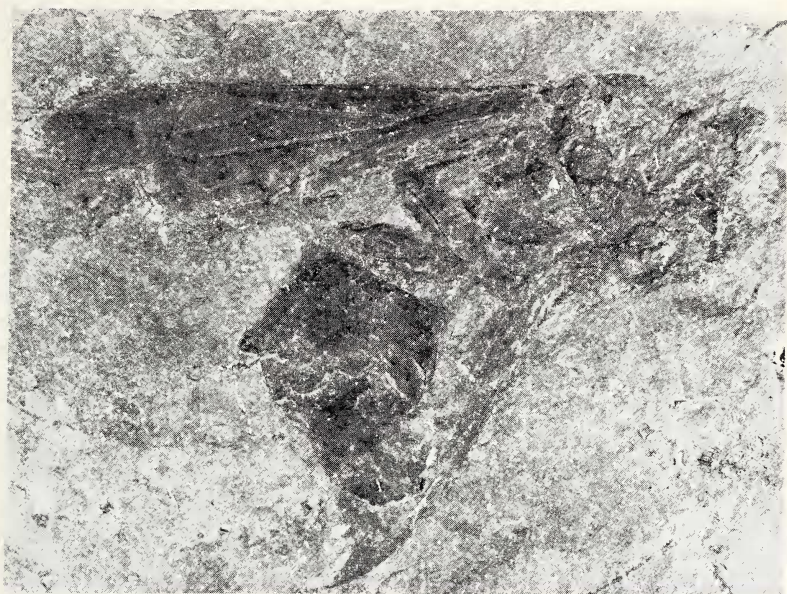
Figure 2.     Vespoid wasp from Eocene of British Columbia. Original photograph
of specimen in Royal Ontario Museum, Toronto. Length of forewing, 12 mm.


Piton (1940), in a thesis on the Eocene fossil beds of Menat,
France, described an assemblage of Vespoidea found in this sedi-
mentary deposit. However, because the six specimens he described
are all assigned to extant genera, and do not show the characters
essential for such generic designation, Piton's taxonomic determina-
tions are perforce questionable. Particularly dubious is his place-
ment of one specimen in the family Vespidae, genus *Polistes*.
Because the morphological features necessary for accurate taxo-
nomic placement are obscured in this fossil, I prefer to place it in
Vespoidea *incertae sedis*. The remaining five specimens are assigned
to the Eumenidae *incertae sedis*.

Another vespoid species was recently recovered from a Middle
Eocene deposit in British Columbia (M. V. H. Wilson, 1977). Al-
though not formally described, the fossil clearly shows the charac-
teristic venation of the vespoid complex (see Fig. 2), but could be
either a vespid or a eumenid. Of course, one has no way of stating

with certainty that these early vespids were social. Within the Vespidae, divisions into subfamily and tribe are based primarily on behavioral rather than morphological characters. Furthermore, the morphological differences between the castes in any given species are often not obvious in the preserved fossils.

*Oligocene*

True vespids are first found in the Upper Oligocene shales of Florissant, Colorado and Rott, Germany, two highly productive fossiliferous deposits. These beds and other various localities listed in Table 3 have turned up an assemblage comprised of four genera and 14 species. It is quite remarkable that three of the four genera represented are extant and this supports the possibility that the Vespidae were essentially modern by the Oligocene. Furthermore, the diversification of taxa suggests a much earlier origin for the family than is evidenced by the fossil record.

*Miocene*

Scarcely any Vespidae are known from the Miocene, although this is most likely due to the overall dearth of deposits from this epoch. One vespid has been described from a deposit in Germany. This is *Polistes kirbyanus* and clearly belongs to the subfamily Polistinae. Other wasps from Miocene deposits have yet to be discovered, but one can assume that the wasp fauna of this age would be barely distinguishable from the wasp fauna of today.

FORMICOIDEA

The following review of the fossil history of the Formicidae provides important information on their dominance, distribution, and supposed habits during the Mesozoic and Cenozoic eras. In contrast to the Vespoidea, ants are the most abundant insects in Tertiary formations. This may be attributed to their foraging behavior on and around trees, which enhances their chances of preservation in amber. A rough total of 20,000 specimens representing some 200 species of ants has been studied (Table 4); this massive amount of work far exceeds the paleontological investigations carried out on any other family of insects. Several comprehensive monographs on the subject have been written, including *The Ants of the Baltic Amber* (Wheeler, 1914), and *The Fossil Ants of North America* (Carpenter, 1930), which are drawn on extensively in the following pages.

*Cretaceous*

The Cretaceous Period has, without question, provided more information on the early evolution of the ants than any other period, primarily because of the discovery in 1967 of two perfectly preserved worker ants in a New Jersey amber deposit. No doubt exists as to the primitive nature of these Cretaceous ants — both are members of the same species, *Sphecomyrma freyi* Wilson and Brown, and possess a mixture of wasp and ant characters. The petiole is distinctly ant-like, although the mandibles, which are short and bidentate, are very wasp-like (see Fig. 3A). A new subfamily, Sphecomyrminae, was named to accommodate *S. freyi* (Wilson, Carpenter, and Brown, 1967), and is considered ancestral to all known formicid subfamilies (see Taylor, 1978).

Since the discovery of *Sphecomyrma*, several other Cretaceous ants have been found, and these provide strong evidence that the family was widespread during this period. Dlussky (1975) described two new genera and three species, *Cretomyrma arnoldii, C. unicornis,* and *Paleomyrmex zherichini* (from a Late Cretaceous amber deposit in Yantardak, USSR) which he assigned to the Sphecomyrminae. It is of interest that the type of *P. zherichini* is the first winged male ant to be found in a Cretaceous deposit and provides the only indication of wing venation in the Sphecomyrminae (Fig. 3B). The figured specimen of *Cretomyrma unicornis* raises doubts as to its position in the Formicidae for it is a badly mangled, poorly preserved specimen and might be better assigned to Hymenoptera *incertae sedis.*[5] A fifth specimen, apparently a worker, has recently been discovered in the Cretaceous amber of Manitoba, Canada. Although not yet described, it undoubtedly belongs to the subfamily Sphecomyrminae (Wilson, personal communication).

*Paleocene*

No ants from the Paleocene are known, undoubtedly because so few fossiliferous beds containing insect remains from this epoch

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[5]Dlussky (1975) also described several other "ants" which were found in Upper Cretaceous deposits in the Kzyl-Zhar of Russia. Three genera (3 species) were placed in the subfamily Ponerinae: *Petropone petiolata, Cretopone magna,* and *Archaeopone kzylzharica.* These are all fragmentary specimens, and, as figured by Dlussky, present no characters which would place them unequivocally in the Formicidae. They much more obviously belong in Hymenoptera *incertae sedis,* as does *Dolichomyrma longiceps* from the Upper Cretaceous of Kzyl-Zhar, which Dlussky put into Formicidae *incertae sedis.*

TABLE 3.   VESPOIDEA IN THE FOSSIL RECORD.

| Geological Age | Locality | References |
|---|---|---|
| CRETACEOUS | | |
| Masaridae | | |
| *Curiovespa curiosa* Rasnitsyn | Kazakh, U.S.S.R. | Rasnitsyn, 1975 |
| *Curiovespa magna* Rasnitsyn | Kazakh, U.S.S.R. | Rasnitsyn, 1975 |
| EOCENE | | |
| Eumenidae | | |
| ?*Alastor solidescens* (Scudder) | Green River, Wyoming | Evans, 1966 |
| ?*Rhygchium andrei* Piton | Menat, France | Piton, 1940 |
| ?*Odynerus manevali* Piton | Menat, France | Piton, 1940 |
| ?*Ancistrocerus eocenicus* Piton | Menat, France | Piton, 1940 |
| ?*Ancistrocerus berlandi* Piton | Menat, France | Piton, 1940 |
| ?*Eumenes projaponica* Piton | Menat, France | Piton, 1940 |
| ?Vespidae | | |
| ?*Polistes vergnei* Piton | Menat, France | Piton, 1940 |
| OLIGOCENE | | |
| Eumenidae | | |
| *Rhynchium* sp. Theobald | Cereste, France | Theobald, 1937 |
| *Odynerus terryi* Cockerell | Florissant, Colorado | Cockerell, 1909a |
| *Odynerus wilmattae* Cockerell | Florissant, Colorado | Cockerell, 1914 |
| *Odynerus oligopunctatus* Theobald | Cereste, France | Theobald, 1937 |
| ?*Odynerus praesulptus* Cockerell | Florissant, Colorado | Cockerell, 1906 |
| *Odynerus percantusus* Cockerell | Florissant, Colorado | Cockerell, 1914 |
| ?*Alastor rottensis* Statz | Rott, Germany | Statz, 1936 |
| "*Pseudonortania*"† *sepulta* Timon-David | Camoins, France | Timon-David, 1944 |

Vespidae

| | | |
|---|---|---|
| ?*Paleovespa gillettei Cockerell | Florissant, Colorado | Bequaert, 1930 |
| ?*Paleovespa florissantia Cockerell | Florissant, Colorado | Bequaert, 1930 |
| ?*Paleovespa scudderi Cockerell | Florissant, Colorado | Bequaert, 1930 |
| ?*Paleovespa relecta Cockerell | Florissant, Colorado | Bequaert, 1930 |
| *Paleovespa baltica Cockerell | Baltic Amber | Cockerell, 1909b |
| *Paleovespa wilsoni Cockerell | Florissant, Colorado | Cockerell, 1914 |
| Polistes industrius Theobald | Cereste, France | Theobald, 1937 |
| Polistes signata Statz | Rott, Germany | Statz, 1936 |
| ?Polybia anglica Cockerell | Isle of Wight, England | Cockerell, 1921a |
| Polybia oblita Cockerell | Isle of Wight, England | Cockerell, 1921b |
| Vespa bilineata Statz | Rott, Germany | Statz, 1936 |
| Vespa cordifera Statz | Rott, Germany | Statz, 1936 |
| Vespa nigra Statz | Rott, Germany | Statz, 1936 |

MIOCENE

Vespidae

| | | |
|---|---|---|
| Polistes kirbyanus Cockerell | Oeningen, Germany | Cockerell, 1914 |
| ?Vespa attavina Heer | Parschlug, Germany | Heer, 1849 |
| ?Vespa crabroniformis Heer | Radoboj, Croatia | Heer, 1867 |

?Of uncertain position within the Vespoidea — clearly Diploptera, but further determination impossible.
†Pseudonortonia Timon-David is a junior homonym of Pseudonortonia Soika, 1936.
*Extinct genera.

TABLE 3. VESPOIOEA IN THE FOSSIL RECORD.

100

| Geological Age | Locality | References |
|---|---|---|
| **CRETACEOUS** | | |
| Masaridae | | |
| *Curiovespa curiosa Rasnitsyn | Kazakh, U.S.S.R. | Rasnitsyn, 1975 |
| *Curiovespa magna Rasnitsyn | Kazakh, U.S.S.R. | Rasnitsyn, 1975 |
| **EOCENE** | | |
| Eumenidae | | |
| ?Alastor solidescens (Scudder) | Green River, Wyoming | Evans, 1966 |
| ?Rhygchium andrei Piton | Menat, France | Piton, 1940 |
| ?Odynerus manevali Piton | Menat, France | Piton, 1940 |
| ?Ancistrocerus eocenicus Piton | Menat, France | Piton, 1940 |
| ?Ancistrocerus berlandi Piton | Menat, France | Piton, 1940 |
| ?Eumenes projaponica Piton | Menat, France | Piton, 1940 |
| ?Vespidae | | |
| ?Polistes vergnei Piton | Menat, France | Piton, 1940 |
| **OLIGOCENE** | | |
| Eumenidae | | |
| Rhynchium sp. Theobald | Cereste, France | Theobald, 1937 |
| Odynerus terryi Cockerell | Florissant, Colorado | Cockerell, 1909a |
| Odynerus wilmattae Cockerell | Florissant, Colorado | Cockerell, 1914 |
| Odynerus oligopunctatus Theobald | Cereste, France | Theobald, 1937 |
| ?Odynerus praesulptus Cockerell | Florissant, Colorado | Cockerell, 1906 |
| Odynerus percantusus Cockerell | Florissant, Colorado | Cockerell, 1914 |
| ?Alastor rottensis Statz | Rott, Germany | Statz, 1936 |
| "Pseudonortania"† sepulta Timon-Oavid | Camoins, France | Timon-Oavid, 1944 |

| | | |
|---|---|---|
| Vespidae | | |
| ?*Paleovespa gillettei Cockerell | Florissant, Colorado | Bequaert, 1930 |
| ?*Paleovespa florissantia Cockerell | Florissant, Colorado | Bequaert, 1930 |
| ?*Paleovespa scudderi Cockerell | Florissant, Colorado | Bequaert, 1930 |
| ?*Paleovespa relecta Cockerell | Florissant, Colorado | Bequaert, 1930 |
| *Paleovespa baltica Cockerell | Baltic Amber | Cockerell, 1909b |
| *Paleovespa wilsoni Cockerell | Florissant, Colorado | Cockerell, 1914 |
| Polistes industrius Theobald | Cereste, France | Theobald, 1937 |
| Polistes signata Statz | Rott, Germany | Statz, 1936 |
| ?Polybia anglica Cockerell | Isle of Wight, England | Cockerell, 1921a |
| Polybia oblita Cockerell | Isle of Wight, England | Cockerell, 1921b |
| Vespa bilineata Statz | Rott, Germany | Statz, 1936 |
| Vespa cordifera Statz | Rott, Germany | Statz, 1936 |
| Vespa nigra Statz | Rott, Germany | Statz, 1936 |
| **MIOCENE** | | |
| Vespidae | | |
| Polistes kirbyanus Cockerell | Oeningen, Germany | Cockerell, 1914 |
| ?Vespa attavina Heer | Parschlug, Germany | Heer, 1849 |
| ?Vespa crabroniformis Heer | Radoboj, Croatia | Heer, 1867 |

?Of uncertain position within the Vespoidea — clearly Oiploptera, but further determination impossible.
†Pseudonortania Timon-Oavid is a junior homonym of Pseudonortania Soika, 1936.
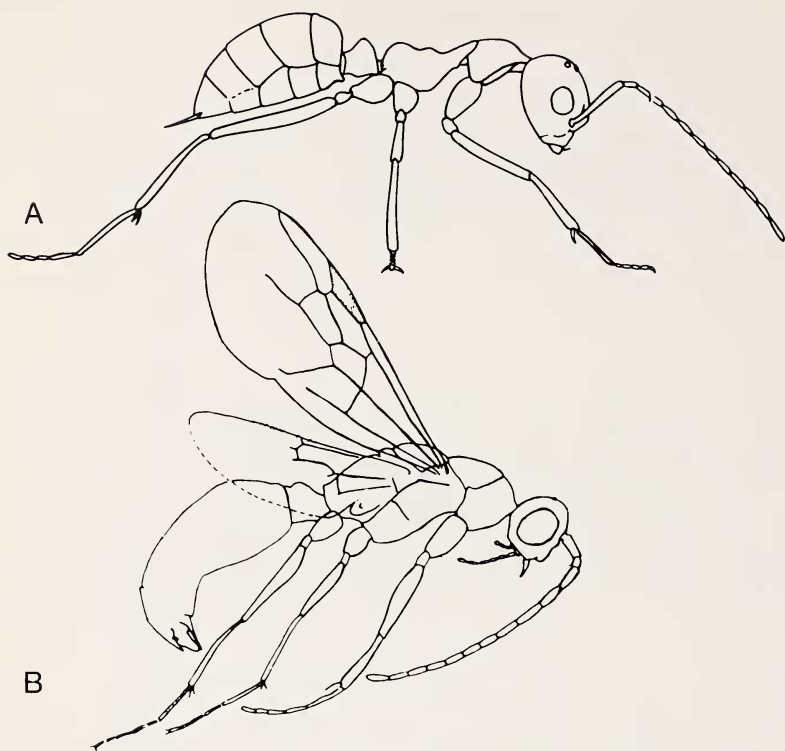*Extinct genera.

Figure 3A. *Sphecomyrma freyi* Wilson and Brown from the lower part of Upper Cretaceous of New Jersey. Drawing of holotype worker in Museum of Comparative Zoology, modified from Wilson, Carpenter, and Brown (1967). Length of body, 3.5 mm.

Figure 3B. *Paleomyrmex zherichini* Rasnitsyn from the lower part of the Upper Cretaceous of U.S.S.R. Drawing of holotype male in Paleontological Institute, Moscow, from Rasnitsyn, 1977. Length of body, 5.4 mm.

have been discovered. Mention is made by Brues (1936) of a piece of petrified wood containing what he considers ant borings, highly resemblant of borings made by *Camponotus* today. Although there is no clear-cut evidence that these borings represent *Camponotus* activity, or insect activity of any kind, it is conceivable that *Camponotus* was present in New Mexico during the Paleocene; several species have been dscribed from the Florissant Shales, Colorado (Upper Oligocene), and one from the Baltic Amber

(Lower Oligocene). In addition, it must be remembered that the Paleocene did not begin for at least 40 million years after the appearance of *Sphecomyrma freyi.*

### Eocene

Very few fossil ants have been found in deposits of this age, and the determinations of many of these ant species are in doubt. Scudder (1877, 1878) described four supposed ants from the Green River formation, and five ants (1877) from the Quesnel Beds in British Columbia. Generic identifications on all of these fossils are to be considered dubious at best, and more likely incorrect (Carpenter, 1930).

In 1920, two species, *Oecophylla bartoniana* and *Formica heteroptera,* were described by Cockerell from an Eocene deposit in Bournemouth, England. Wheeler (1928) considered these ants formicines, but because the descriptions were based on wing fragments, he questioned their generic determinations. Similarly, Cockerell's *Formica eoptera* (1923a) from the Eocene of Texas is of uncertain position at both the generic and subfamily levels. *Archimyrmex rostratus* (Cockerell, 1923b) from the Eocene shales of Colorado is probably a myrmicine (Carpenter, 1930), and is the only Green River ant that can be placed with any certainty in a subfamily. Carpenter (1929) described *Eoponera berryi* from the Wilcox formation of Tennessee, and placed this ant in the subfamily Ponerinae. He suggests that it may be closely allied to the Neotropical genus *Dinoponera.* This is of interest because *Eoponera berryi* is the oldest known ant (Lower Eocene) to be assigned to a living subfamily of Formicidae.

Wilson (personal communication) mentions the recent discovery of three ants in a Middle Eocene amber deposit near Malvern, Arkansas, each belonging to a different subfamily. One belongs to the Dolichoderinae, genus *Iridomyrmex;* one is a formicine closely allied to the genus *Paratrechina,* and considered a relatively primitive, or "typical euformicine"; the last is a new genus of myrmicine, unique by virtue of its inflated postpetiole. These ants have yet to be formally described but they are nevertheless of paramount interest. The presence of these subfamilies in North America in the Eocene is strongly suggestive of their rapid evolution and dispersal during the Paleocene and perhaps during the Cretaceous.

*Oligocene*

The Baltic Amber is, most certainly, the best studied of all Tertiary insect deposits, and has revealed a great deal about the nature and diversity of Oligocene ants.[6] As of 1928, 11,711 ants (93 species) were examined from this deposit. Of this number, 1461 were studied by Mayr (1868); 690 by André (1895); and 9,560 by Wheeler (1914, 1928).

An examination of the ant fauna reveals wide representation at the subfamily and generic levels. All extant subfamilies of Formicidae are found in the amber with the exception of the Dorylinae and Leptanillinae. The absence of the Dorylinae is probably not due to selective exclusion on the part of the amber, but more likely indicates their absence from that part of the European continent during the Oligocene. Wheeler (1914) speculates that the foraging behavior of doryline ants should readily lead to entrapment in tree resin, but, in all probability, this group was then, as it is now, confined to the tropics. It is not surprising that the Leptanillinae are absent from the Baltic Amber; this is a small subfamily once considered a tribe of the Dorylinae, consisting of one genus and a few species; and although pantropical is hypogaeic and rarely encountered.

The Dolichoderinae and Formicinae together constitute 97 percent of all specimens and evidence indicates that these amber ants were already extraordinarily specialized. Workers of *Iridomyrmex goepperti* were found in a piece of amber (originally in the Königsberg collection) with several aphids. On the basis of this discovery, Wheeler (1914) concludes that Homoptera were attended by ants then much as they are today. The finding of several genera of paussid beetles (e.g., *Arthropterus, Cerapterites* and *Eopaussus*) in the Baltic Amber (Wasmann, 1929) suggests that myrmecophiles were established at this time. Perhaps most remarkable of all was the discovery of two *Lasius schiefferdeckeri* workers — each found with a mite attached to the base of the hind tibia, in precisely the

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[6]Because the Baltic Amber was secondarily deposited in a clay bed of Lower Oligocene age, it is necessarily older than the glauconitic sand ("blue-earth" clay) in which it lies. How much older is uncertain. In some published accounts it is referred to as Eocene. However, since the composition of the Baltic Amber ant fauna is very similar to that of the Florissant Shales and other *bona fide* Oligocene deposits, I am following Zeuner (1939, p. 26) in referring to the amber as Lower Oligocene.

same position on each. This demonstrates almost certainly that by the Lower Oligocene mites had acquired distinct preferences for attachment on specific regions of their host's integument.

Almost as valuable as the Baltic Amber in providing a large and diverse assemblage of fossil ants is the Upper Oligocene deposit in Florissant, Colorado, studied by Carpenter (1930). The ant fauna of this deposit is strikingly similar to that of the Baltic Amber in many respects. It is interesting to note that roughly the same percentage of extant genera is found in both places; in the Florissant Shales this figure is given as 60 percent (Carpenter, 1930), in the Baltic Amber 56 percent (Wheeler, 1914). *Iridomyrmex* is clearly a dominant genus in the Baltic Amber, and although not so common in the Florissant Shales, a closely allied genus, *Protazteca,* comprises more than 25 percent of all specimens (Brown, 1973).

Another similarity between the two deposits is the relative percentages of the various subfamilies. As in the amber, the Dolichoderinae are predominant, comprising 60 percent of the total number of ants. The Formicinae comprise another 25 to 30 percent, and the Myrmicinae in each deposit are represented by five percent or less of the total specimens. This suggests that the ant fauna in the northern hemisphere was essentially homogenous during the Oligocene.

The remaining deposits of Oligocene age from which ants have been described are of relatively minor importance. Most of the specimens are fragmentary and the determinations dubious; nevertheless, a mention of them is certainly necessary. Specimens from Gurnet Bay, Isle of Wight, England, have been studied by Cockerell (1915) and Donisthorpe (1920). Cockerell described eight species of ants from this deposit but, because his generic determinations are based chiefly on highly variable measurements of wing fragments, they are of dubious significance. Donisthorpe examined a total of eight genera and fourteen species belonging to the subfamilies Ponerinae, Dolichoderinae, and Formicinae. Surprising is the large number of *Oecophylla* workers recovered (245); this genus is now restricted to Africa, India, and Australia, and is much more numerous in the Gurnet Bay deposit than in the Baltic Amber or Florissant Shales. This might be due to the difference in latitude between the deposits which would account for a warmer climate at Gurnet Bay later into the Tertiary than at the more northern deposits.

Another Lower Oligocene deposit which has provided beautifully preserved fossil ants is Aix-en-Provence, France. Several species have been described by Theobald (1937), who recognized four subfamilies: Myrmicinae (1 species); Ponerinae (1 species); Dolichoderinae (1 genus, 2 species); and Formicinae (3 genera, 9 species). Also described by Theobald (1937) is an Oligocene collection from Haut-Rhin, France, in which he recognizes the same four subfamilies (16 genera, 34 species). This fauna is very similar to that found in the Baltic Amber; in fact, Theobald has found five species which he considers identical to species in the Baltic Amber. In a deposit in Gard, France, Theobald (1937) describes two species, one a myrmicine, the other a dolichoderine.

Meunier (1917) has described four ant species from an Upper Oligocene deposit in Rott, Germany. These have been assigned to three genera: *Formica, Ponera,* and *Myrmica.* The specimens are well-preserved, as may be seen in Meunier's photographs, but his generic determinations are questionable.

In 1957, two female reproductives of the same species were discovered in an Upper Oligocene deposit in Argentina. The authors described the species as *Ameghinoia piatnitskyi* and placed it in the subfamily Ponerinae (Viana and Haedo-Rossi, 1957). E. O. Wilson (personal communication) is highly sceptical of the placement of *A. piatnitskyi* in the Ponerinae, and thinks that it is very clearly a myrmeciine. This is quite extraordinary because no other fossil ants have been recovered from South America, and more importantly, if Wilson is correct, this is the first indication that the Myrmiciinae were so widespread by the Oligocene.

*Miocene*

The deposits of Miocene age which have provided the greatest number of ant specimens have been the Oeningen beds in Germany, and the Radoboj formation in Croatia. Approximately 60 species of ants from these places were described by the Swiss myrmecologist Heer (1849, 1856, 1867), but his generic assignments are necessarily questionable in terms of present-day concepts of a formicid genus. Regrettably, the type specimens which are essential to a revision of this fossil fauna are believed to be lost.

A few species were described by Emery (1891) in Sicilian amber, presumed to be Miocene, but these, like the specimens studied by Heer, are of questionable generic position.[7]

Another Miocene amber deposit has been found in Chiapas, Mexico, from which some one hundred ants have been recovered. Unfortunately, the majority of these are fragmentary, or otherwise too poor for determination. The assemblage does, however, suggest that the ant fauna in Mexico during the Miocene was essentially the same as might be found in that region today (Brown, 1973).

Fujiyama (1970) described a single ant from the Chōjabaru formation in Japan (middle Miocene) which he named *Aphaenogaster axila,* thought to be closely allied to the subgenus *Deromyrma.* This is not particularly unusual inasmuch as *Aphaenogaster* is a world-wide genus, and several species are found in Japan today.

Perhaps the most interesting of all Miocene material is an ant colony of *Oecophylla leakeyi* found in Kenya (Wilson and Taylor, 1964). This is the first record of an actual, although fragmented, ant colony and contains a total of 366 specimens: 197 larvae, 105 worker pupae, and at least 64 workers. No Nearctic fossils of *Oecophylla* are known, but the species is well represented in European Tertiary deposits. Wilson and Taylor suggest on the basis of these fossil specimens that *Oecophylla* is a morphologically stable paleotropical genus which has persisted through most of the Tertiary with very little specialization.

<center>APOIDEA</center>

The Apoidea form an interesting complex of social insects. Unlike the other social insect groups that are consistent in their degree of social achievement at the ordinal level (Isoptera), family level (Formicidae), and virtually the subfamily level (Vespinae), the Apoidea present a wide spectrum of social behavior at the generic level. Evidence suggests that eusociality has arisen in the bees at least eight times (Michener, 1962; Wilson, 1971), which may explain this variance. Nevertheless, it is noteworthy that of roughly 20,000 existing species of bees only a small minority are thought to be presocial and eusocial (Wilson, 1971). Why sociality in the Apoidea

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[7]These generic determinations are currently being reviewed by Dr. W. L. Brown, Jr.

TABLE 4. FORMICOIDEA IN THE FOSSIL RECORD.

| Geological Age | Locality | References |
|---|---|---|
| CRETACEOUS | | |
| Sphecomyrminae | | |
| *Sphecomyrma freyi Wilson and Brown | New Jersey, U.S.A. | Wilson, Carpenter and Brown, 1967 |
| ?*Sphecomyrma sp. | Manitoba, Canada | Wilson, pers. comm. |
| *Cretomyrma arnoldii Dlussky | Taymyr, U.S.S.R. | Rasnitsyn, 1975 |
| *Cretomyrma unicornis Dlussky | Taymyr, U.S.S.R. | Rasnitsyn, 1975 |
| *Paleomyrmex zherichini Dlussky | Taymyr, U.S.S.R. | Rasnitsyn, 1975 |
| EOCENE | | |
| Myrmicinae | | |
| *Archimyrmex rostratus Cockerell | Florissant, Colorado | Carpenter, 1930 |
| Formicinae | | |
| Oecophylla bartoniana Cockerell | Bournemouth, England | Cockerell, 1920 |
| Formica eoptera Cockerell | Texas, U.S.A. | Carpenter, 1930 |
| Formica heteroptera Cockerell | Bournemouth, England | Cockerell, 1920 |
| ?Paratrechina sp. | Arkansas, U.S.A. | Wilson, pers. comm. |
| Ponerinae | | |
| *Eoponera berryi Carpenter | Tennessee, U.S.A. | Carpenter, 1929 |
| Dolichoderinae | | |
| Iridomyrmex sp. | Arkansas, U.S.A. | Wilson, pers. comm. |
| OLIGOCENE | | |
| Myrmiciinae | | |
| *Ameghinoia piatnitskyi Viana and Haedo-Rossi | Argentina | Viana and Haedo-Rossi, 1957 |
| Ponerinae | | |
| Brachyponera dubia Theobald | Haut-Rhin, Germany | Theobald, 1937a |

| | | |
|---|---|---|
| *Archiponera wheeleri* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Prionomyrmex longiceps* Mayr | Baltic Amber | Wheeler, 1914 |
| *Procerapachys annosus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Procerapachys favosus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Bradoponera meieri* Mayr | Baltic Amber | Wheeler, 1914 |
| Ectatomma europaeum Mayr | Baltic Amber | Wheeler, 1914 |
| *Electoponera dubia* Wheeler | Baltic Amber | Wheeler, 1914 |
| Platythyrea primaeva Wheeler | Baltic Amber | Wheeler, 1914 |
| Euponera calcarea Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| Euponera succinea (Mayr) | Baltic Amber | Wheeler, 1914 |
| Euponera crawleyi Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| Euponera globiventris Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| Ponera atavia Mayr | Baltic Amber | Wheeler, 1914 |
| Ponera minuta Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| Ponera elegantissima Meunier | Rott, Germany | Meunier, 1923 |
| Ponera hypolitha Cockerell | Isle of Wight, England | Cockerell, 1915 |
| Ponera rhenana Meunier | Rott, Germany | Meunier, 1917 |
| ?Ponera gracilicornis Mayr | Baltic Amber | Wheeler, 1914 |
| *Emplastus emeryi Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| *Syntaphus wheeleri Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| Pseudomyrmicinae | | |
| Pseudomyrma extincta Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Myrmicinae | | |
| Aphaenogaster mayri Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Aphaenogaster donisthorpei Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Aphaenogaster maculipes Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| Aphaenogaster maculata Theobald | Aix-en-Provence, France | Theobald, 1937 |
| Aphaenogaster sommerfeldti Mayr | Baltic Amber | Wheeler, 1914 |
| Aphaenogaster oligocenica Wheeler | Baltic Amber | Wheeler, 1914 |

TABLE 4 FORMICOIDEA IN THE FOSSIL RECORD

| Geological Age | Locality | References |
|---|---|---|
| **CRETACEOUS** | | |
| Sphecomyrminae | | |
| •*Sphecomyrma freyi* Wilson and Brown | New Jersey, U.S.A | Wilson, Carpenter and Brown, 1967 |
| ?•*Sphecomyrma* sp. | Manitoba, Canada | Wilson, pers. comm. |
| •*Cretomyrma arnoldii* Dlussky | Taymyr, U.S.S.R. | Rasnitsyn, 1975 |
| •*Cretomyrma unicornis* Dlussky | Taymyr, U.S.S.R | Rasnitsyn, 1975 |
| •*Paleomyrmex zherichini* Dlussky | Taymyr, U.S.S.R. | Rasnitsyn, 1975 |
| **EOCENE** | | |
| Myrmicinae | | |
| •*Archimyrmex rostratus* Cockerell | Florissant, Colorado | Carpenter, 1930 |
| Formicinae | | |
| *Oecophylla bartoniana* Cockerell | Bournemouth, England | Cockerell, 1920 |
| *Formica eoptera* Cockerell | Texas, U.S.A. | Carpenter, 1930 |
| *Formica heteroptera* Cockerell | Bournemouth, England | Cockerell, 1920 |
| ?*Paratrechina* sp. | Arkansas, U.S.A | Wilson, pers comm. |
| Ponerinae | | |
| •*Eoponera berryi* Carpenter | Tennessee, U.S.A. | Carpenter, 1929 |
| Dolichoderinae | | |
| *Iridomyrmex* sp. | Arkansas, U.S.A. | Wilson, pers. comm. |
| **OLIGOCENE** | | |
| Myrmiciinae | | |
| •*Ameghinoia piatnitskya* Viana and Haedo-Rossi | Argentina | Viana and Haedo-Rossi, 1957 |
| Ponerinae | | |
| *Brachyponera dubia* Theobald | Haut-Rhin, Germany | Theobald, 1937a |

| | | |
|---|---|---|
| •*Archiponera wheeleri* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| •*Prionomyrmex longiceps* Mayr | Baltic Amber | Wheeler, 1914 |
| •*Procerapachys annosus* Wheeler | Baltic Amber | Wheeler, 1914 |
| •*Procerapachys favosus* Wheeler | Baltic Amber | Wheeler, 1914 |
| •*Bradoponera meieri* Mayr | Baltic Amber | Wheeler, 1914 |
| *Ectatomma europaeum* Mayr | Baltic Amber | Wheeler, 1914 |
| •*Electoponera dubia* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Platythyrea primaeva* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Euponera calcarea* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Euponera succinea* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Euponera crawleyi* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| *Euponera globiventris* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Ponera atavia* Mayr | Baltic Amber | Wheeler, 1914 |
| *Ponera minuta* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| *Ponera elegantissima* Meunier | Rott, Germany | Meunier, 1923 |
| *Ponera hypolitha* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Ponera rhenana* Meunier | Rott, Germany | Meunier, 1917 |
| ?*Ponera gracilicornis* Mayr | Baltic Amber | Wheeler, 1914 |
| •*Emplastus emeryi* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| •*Syntaphus wheeleri* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| Pseudomyrmicinae | | |
| *Pseudomyrma extincta* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Myrmicinae | | |
| *Aphaenogaster mayri* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Aphaenogaster donisthorpei* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Aphaenogaster maculipes* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Aphaenogaster maculata* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Aphaenogaster sommerfeldti* Mayr | Baltic Amber | Wheeler, 1914 |
| *Aphaenogaster oligocenica* Wheeler | Baltic Amber | Wheeler, 1914 |

TABLE 4. (CONTINUED)

| Geological Age | Locality | References |
|---|---|---|
| OLIGOCENE Myrmicinae (continued) | | |
| *Aphaenogaster mersa* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Sima klebsi* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Sima ocellata* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima simplex* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima angustata* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima lacrimarum* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima klebsi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Sima oligocenica* Theobald | Gard, France | Theobald, 1937 |
| *Monomorium pilipes* Mayr | Baltic Amber | Wheeler, 1914 |
| *Monomorium mayrianum* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Erebomyrma antiqua* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Erebomyrma thorali* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Vollenhovia beyrichi* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Vollenhovia prisca* (Andre) | Baltic Amber | Wheeler, 1914 |
| *Stenamma berendti* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Electromyrmex klebsi* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Agroecomyrmex duisburgi* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Myrmica longispinosa* Mayr | Baltic Amber | Wheeler, 1914 |
| *Myrmica archaica* Meunier | Rott, Germany | Meunier, 1915 |
| *Nothomyrmica rudis* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Nothomyrmica intermedia* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Nothomyrmica rugosostriata* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Nothomyrmica petiolata* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Leptothorax gracilis* Mayr | Baltic Amber | Wheeler, 1914 |

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|---|---|---|
| *Leptothorax glaesarius* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax longaevus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax hystriculus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax placivus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax gurnetensis* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Leucotaphus cockerelli* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| \**Stiphromyrmex robustus* (Mayr) | Baltic Amber | Wheeler, 1914 |
| \**Parameranoplus primaevus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Stigmomyrmex venustus* Mayr | Baltic Amber | Wheeler, 1914 |
| \**Enneamerus reticulatus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Solenopsis maxima* (Förster) | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis valida* (Förster) | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis major* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis superba* Förster | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis försteri* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis blanda* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Pheidole tertiaria* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Messor sculpteratus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Pogonomyrmex fossilis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Lithomyrmex rugosus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Lithomyrmex striatus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| \**Cephalomyrmex rotundatus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Dolichoderinae | | |
| \**Protaneuretus succineus* Wheeler | Baltic Amber | Wheeler, 1914 |
| \**Paraneuretus tornquisti* Wheeler | Baltic Amber | Wheeler, 1914 |
| \**Paraneuretus longipennis* Wheeler | Baltic Amber | Wheeler, 1914 |
| \**Mianeuretus mirabilis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Dolichoderus oviformis* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dolichoderus coquandi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |

TABLE 4 (CONTINUED)

| Geological Age | Locality | References |
|---|---|---|
| OLIGOCENE Myrmicinae (continued) | | |
| *Aphaenogaster mersa* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Sima klebsi* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Sima ocellata* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima simplex* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima angustata* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima lacrimarum* Mayr | Baltic Amber | Wheeler, 1914 |
| *Sima klebsi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Sima oligocenica* Theobald | Gard, France | Theobald, 1937 |
| *Monomorium pilipes* Mayr | Baltic Amber | Wheeler, 1914 |
| *Monomorium mayrianum* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Erebomyrma antiqua* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Erebomyrma thorali* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Vollenhovia beyrichi* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Vollenhovia prisca* (Andre) | Baltic Amber | Wheeler, 1914 |
| *Stenamma berendti* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Electromyrmex klebsi* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Agroecomyrmex duisburgi* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Myrmica longispinosa* Mayr | Baltic Amber | Wheeler, 1914 |
| *Myrmica archaica* Meunier | Rott, Germany | Meunier, 1915 |
| *Nothomyrmica rudis* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Nothomyrmica intermedia* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Nothomyrmica rugosostriata* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Nothomyrmica petiolata* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Leptothorax gracilis* Mayr | Baltic Amber | Wheeler, 1914 |

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|---|---|---|
| *Leptothorax glaesarius* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax longaevus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax hystriculus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax placivus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Leptothorax gurnetensis* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Leucotaphus cockerelli* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| *Stiphromyrmex robustus* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Parameranoplus primaevus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Stigmomyrmex venustus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Enneamerus reticulatus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Solenopsis maxima* (Förster) | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis valida* (Forster) | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis major* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis superba* Förster | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis försteri* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Solenopsis blanda* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Pheidole tertiaria* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Messor sculpteratus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Pogonomyrmex fossilis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Lithomyrmex rugosus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Lithomyrmex striatus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Cephalomyrmex rotundatus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Dolichoderinae | | |
| *Protaneuretus succineus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Paraneuretus tornquisti* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Paraneuretus longipennis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Mianeuretus mirabilis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Dolichoderus oviformis* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dolichoderus coquandi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |

TABLE 4. (CONTINUED)

| Geological Age | Locality | References |
|---|---|---|
| OLIGOCENE Dolichoderinae (continued) | | |
| *Dolichoderus bruneti* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dolichoderus explicans* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dolichoderus affectus* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dolichoderus balticus* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Dolichoderus balticus* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus oviformis* Theobald | Gard, France | Theobald, 1937 |
| *Dolichoderus antiquus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Dolichoderus rohweri* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Dolichoderus cornutus* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus passalomma* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus elegans* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus mesosternalis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus vexillarius* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus sculpteratus* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus tertiarius* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus longipennis* Mayr | Baltic Amber | Wheeler, 1914 |
| *Dolichoderus britannicus* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Dolichoderus gurnetensis* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| *Dolichoderus ovigerus* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Dolichoderus vectensis* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| *Iridomyrmex goepperti* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Iridomyrmex goepperti* Mayr | Baltic Amber | Wheeler, 1914 |
| *Iridomyrmex geinitzi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Iridomyrmex geinitzi* (Mayr) | Baltic Amber | Wheeler, 1914 |

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| *Iridomyrmex breviantennis* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Iridomyrmex florissantius* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Iridomyrmex obscurans* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Iridomyrmex constrictus* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Iridomyrmex samlandicus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Iridomyrmex oblongiceps* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Protazteca elongata* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Protazteca quadrata* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Protazteca capitata* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Liometopum miocenicum* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Liometopum oligocenicum* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Liometopum scudderi* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Elaeomyrmex gracilis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Elaeomyrmex coloradensis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Asymphylomyrmex balticus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Pityomyrmex tornquisti* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Miomyrmex impactus* (Cockerell) | Florissant, Colorado | Carpenter, 1930 |
| *Miomyrmex striatus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Petraeomyrmex minimus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| Formicinae | | |
| *Plagiolepis succini* André | Baltic Amber | Wheeler, 1914 |
| *Plagiolepis klinsmanni* Mayr | Baltic Amber | Wheeler, 1914 |
| *Plagiolepis kuenowi* Mayr | Baltic Amber | Wheeler, 1914 |
| *Plagiolepis squamifera* Mayr | Baltic Amber | Wheeler, 1914 |
| *Plagiolepis singularis* Mayr | Baltic Amber | Wheeler, 1914 |
| *Plagiolepis solitaria* Mayr | Baltic Amber | Wheeler, 1914 |
| *Rhopalomyrmex pygmaeus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Dimorphomyrmex theryi* Emery | Baltic Amber | Wheeler, 1914, 1929 |
| *Dimorphomyrmex mayri* Wheeler | Baltic Amber | Wheeler, 1914 |

TABLE 4 (CONTINUED)

| Geological Age | Locality | References |
|---|---|---|

OLIGOCENE Dolichoderinae (continued)
*Dolichoderus bruneti* Theobald — Haut-Rhin, Germany — Theobald, 1937
*Dolichoderus explicans* Theobald — Haut-Rhin, Germany — Theobald, 1937
*Dolichoderus affectus* Theobald — Haut-Rhin, Germany — Theobald, 1937
*Dolichoderus balticus* Theobald — Aix-en-Provence, France — Theobald, 1937
*Dolichoderus balticus* (Mayr) — Baltic Amber — Wheeler, 1914
*Dolichoderus oviformis* Theobald — Gard, France — Theobald, 1937
*Dolichoderus antiquus* Carpenter — Florissant, Colorado — Carpenter, 1930
*Dolichoderus rohweri* Carpenter — Florissant, Colorado — Carpenter, 1930
*Dolichoderus cornutus* (Mayr) — Baltic Amber — Wheeler, 1914
*Dolichoderus passalomma* Wheeler — Baltic Amber — Wheeler, 1914
*Dolichoderus elegans* Wheeler — Baltic Amber — Wheeler, 1914
*Dolichoderus mesosternalis* Wheeler — Baltic Amber — Wheeler, 1914
*Dolichoderus vexillarius* Wheeler — Baltic Amber — Wheeler, 1914
*Dolichoderus sculpteratus* (Mayr) — Baltic Amber — Wheeler, 1914
*Dolichoderus tertiarius* (Mayr) — Baltic Amber — Wheeler, 1914
*Dolichoderus longipennis* Mayr — Baltic Amber — Wheeler, 1914
*Dolichoderus britannicus* Cockerell — Isle of Wight, England — Cockerell, 1915
*Dolichoderus gurnetensis* Donisthorpe — Isle of Wight, England — Donisthorpe, 1920
*Dolichoderus ovigerus* Cockerell — Isle of Wight, England — Cockerell, 1915
*Dolichoderus vectensis* Donisthorpe — Isle of Wight, England — Donisthorpe, 1920
*Iridomyrmex goepperti* Theobald — Haut-Rhin, Germany — Theobald, 1937
*Iridomyrmex goepperti* Mayr — Baltic Amber — Wheeler, 1914
*Iridomyrmex geinitzi* Theobald — Haut-Rhin, Germany — Theobald, 1937
*Iridomyrmex geinitzi* (Mayr) — Baltic Amber — Wheeler, 1914

*Iridomyrmex breviantennis* Theobald — Haut-Rhin, Germany — Theobald, 1937
*Iridomyrmex florissantius* Carpenter — Florissant, Colorado — Carpenter, 1930
*Iridomyrmex obscurans* Carpenter — Florissant, Colorado — Carpenter, 1930
*Iridomyrmex constrictus* (Mayr) — Baltic Amber — Wheeler, 1914
*Iridomyrmex samlandicus* Wheeler — Baltic Amber — Wheeler, 1914
*Iridomyrmex oblongiceps* Wheeler — Baltic Amber — Wheeler, 1914
*Protazteca elongata* Carpenter — Florissant, Colorado — Carpenter, 1930
*Protazteca quadrata* Carpenter — Florissant, Colorado — Carpenter, 1930
*Protazteca capitata* Carpenter — Florissant, Colorado — Carpenter, 1930
*Liometopum miocenicum* Carpenter — Florissant, Colorado — Carpenter, 1930
*Liometopum oligocenicum* Wheeler — Baltic Amber — Wheeler, 1914
*Liometopum scudderi* Carpenter — Florissant, Colorado — Carpenter, 1930
*Elaeomyrmex gracilis* Carpenter — Florissant, Colorado — Carpenter, 1930
*Elaeomyrmex coloradensis* Carpenter — Florissant, Colorado — Carpenter, 1930
*Asymphylomyrmex balticus* Wheeler — Baltic Amber — Wheeler, 1914
*Pityomyrmex tornquisti* Wheeler — Baltic Amber — Wheeler, 1914
*Miomyrmex impactus* (Cockerell) — Florissant, Colorado — Carpenter, 1930
*Miomyrmex striatus* Carpenter — Florissant, Colorado — Carpenter, 1930
*Petraeomyrmex minimus* Carpenter — Florissant, Colorado — Carpenter, 1930
Formicinae
*Plagiolepis succini* André — Baltic Amber — Wheeler, 1914
*Plagiolepis klinsmanni* Mayr — Baltic Amber — Wheeler, 1914
*Plagiolepis kuenowi* Mayr — Baltic Amber — Wheeler, 1914
*Plagiolepis squamifera* Mayr — Baltic Amber — Wheeler, 1914
*Plagiolepis singularis* Mayr — Baltic Amber — Wheeler, 1914
*Plagiolepis solitaria* Mayr — Baltic Amber — Wheeler, 1914
\*Rhopalomyrmex pygmaeus* Mayr — Baltic Amber — Wheeler, 1914
*Dimorphomyrmex theryi* Emery — Baltic Amber — Wheeler, 1914, 1929
*Dimorphomyrmex mayri* Wheeler — Baltic Amber — Wheeler, 1914

TABLE 4. (CONTINUED)

| Geological Age | Locality | References |
|---|---|---|
| OLIGOCENE Formicinae (continued) | | |
| *Gesomyrmex annectens* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Gesomyrmex expectans* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Gesomyrmex miegi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Gesomyrmex hoernesi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Gesomyrmex hoernesi* Mayr | Baltic Amber | Wheeler, 1929 |
| *Prodimorphomyrmex primigenius* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Oecophylla superba* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Oecophylla brischkei* Mayr | Baltic Amber | Wheeler, 1914 |
| *Oecophylla brevinodis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Oecophylla megarche* Cockerell | Isle of Wight, England | Donisthorpe, 1920 |
| *Oecophylla atavina* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Oecophylla perdita* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Prenolepis henschei* Mayr | Baltic Amber | Wheeler, 1914 |
| *Prenolepis pygmaea* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius schiefferdeckeri* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius pumilus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius epicentrus* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Lasius chambonensis* Piton and Theobald | Lac Chambon, France | Piton and Theobald, 1935 |
| *Lasius tertiarius* Zalessky | Ukraine, U.S.S.R. | Zalessky, 1949 |
| *Lasius punctulatus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius nemorivagus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Lasius edentatus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Tetramorium peritulus* (Cockerell) | Florissant, Colorado | Wilson, 1955 |
| *Eoformica eocenica* Cockerell | Florissant, Colorado | Cockerell, 1921c |

| Species | Location | Reference |
|---|---|---|
| *Formica flori* Mayr | Baltic Amber | Wheeler, 1914 |
| *Formica flori* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Formica horrida* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica phaethusa* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica clymene* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica constricta* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Formica strangulata* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica tripartita* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Formica alsatica* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Formica serresi* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica latinodosa* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica oculata* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica minutula* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica sepulta* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica robusta* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Formica cockerelli* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Formica grandis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Formica masculipennis* Piton and Theobald | Auxillac, France | Piton and Theobald, 1935 |
| *Formica pitoni* Theobald | Lac Chambon, France | Piton and Theobald, 1935 |
| *Formica bauckhorni* Meunier | Rott, Germany | Meunier, 1917 |
| *Formica auxillacensis* Piton and Theobald | Auxillac, France | Piton and Theobald, 1935 |
| *Glaphyomyrmex oligocenicus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Pseudolasius boreus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dryomyrmex fuscipennis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dryomyrmex fuscipennis* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dryomyrmex claripennis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Glaphyromyrmex oligocenicus* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Camponotus mengei* Mayr | Baltic Amber | Wheeler, 1914 |
| *Camponotus mengei* Theobald | Haut-Rhin, Germany | Theobald, 1937 |

TABLE 4. (CONTINUED)

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| Geological Age | Locality | References |
|---|---|---|
| OLIGOCENE Formicinae (continued) | | |
| *Gesomyrmex annectens* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Gesomyrmex expectans* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Gesomyrmex miegi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Gesomyrmex hoernesi* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Gesomyrmex hoernesi* Mayr | Baltic Amber | Wheeler, 1929 |
| • *Prodimorphomyrmex primigemus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Oecophylla superba* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Oecophylla brischkei* Mayr | Baltic Amber | Wheeler, 1914 |
| *Oecophylla brevinodis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Oecophylla megarche* Cockerell | Isle of Wight, England | Donisthorpe, 1920 |
| *Oecophylla atavina* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Oecophylla perdita* Cockerell | Isle of Wight, England | Cockerell, 1915 |
| *Prenolepis henschei* Mayr | Baltic Amber | Wheeler, 1914 |
| *Prenolepis pygmaea* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius schefferdeckeri* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius pumilus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius epicentrus* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Lasius chambonensis* Piton and Theobald | Lac Chambon, France | Piton and Theobald, 1935 |
| *Lasius tertiarius* Zalessky | Ukraine, U.S.S.R. | Zalessky, 1949 |
| *Lasius punctulatus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Lasius nemorivagus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Lasius edentatus* Mayr | Baltic Amber | Wheeler, 1914 |
| *Tetramorium peritulus* (Cockerell) | Florissant, Colorado | Wilson, 1955 |
| *Eoformica eocenica* Cockerell | Florissant, Colorado | Cockerell, 1921c |
| *Formica flori* Mayr | Baltic Amber | Wheeler, 1914 |
| *Formica flori* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Formica horrida* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica phaethusa* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica clymene* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica constricta* (Mayr) | Baltic Amber | Wheeler, 1914 |
| *Formica strangulata* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Formica tripartita* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Formica alsatica* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Formica serresi* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica latinodosa* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica oculata* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica minutula* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica sepulta* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Formica robusta* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Formica cockerelli* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Formica grandis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Formica masculipennis* Piton and Theobald | Auxillac, France | Piton and Theobald, 1935 |
| *Formica piton* Theobald | Lac Chambon, France | Piton and Theobald, 1935 |
| *Formica bauckhorni* Meunier | Rott, Germany | Meunier, 1917 |
| *Formica auxillacensis* Piton and Theobald | Auxillac, France | Piton and Theobald, 1935 |
| *Glaphyomyrmex oligocenicus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Pseudolasius boreus* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dryomyrmex fuscipennis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Dryomyrmex fuscipennis* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Dryomyrmex claripennis* Wheeler | Baltic Amber | Wheeler, 1914 |
| *Glaphyomyrmex oligocenicus* Theobald | Haut-Rhin, Germany | Theobald, 1937 |
| *Camponotus mengei* Mayr | Baltic Amber | Wheeler, 1914 |
| *Camponotus mengei* Theobald | Haut-Rhin, Germany | Theobald, 1937 |

TABLE 4. (CONCLUDED)

| Geological Age | Locality | References |
|---|---|---|
| OLIGOCENE Formicinae (continued) | | |
| *Camponotus vehemens* Förster | Haut-Rhin, Germany | Theobald, 1937 |
| *Camponotus longiventris* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Camponotus saussurei* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Camponotus penninervis* Theobald | Aix-en-Provence, France | Theobald, 1937 |
| *Camponotus fuscipennis* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Camponotus microcephalus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Camponotus petrifactus* Carpenter | Florissant, Colorado | Carpenter, 1930 |
| *Camponotus brodiei* Donisthorpe | Isle of Wight, England | Donisthorpe, 1920 |
| MIOCENE | | |
| Ponerinae | | |
| *Ponera umbra* Popov | Caucasus, U.S.S.R. | Popov, 1933 |
| Myrmicinae | | |
| *Aphaenogaster axila* Fujiyama | Chôjabaru, Japan | Fujiyama, 1970 |
| Formicinae | | |
| *Camponotus obesus* Piton | Joursac, France | Piton and Theobald, 1935 |
| *Camponotus tokunagai* Naora | China | Naora, 1933 |
| *\*Pseudocamponotus elkoanus* Carpenter | Elko, Nevada | Carpenter, 1930 |
| *Solenopsis longaevus* Heer | Radoboj, Croatia | Poncracz, 1928 |
| *Formica cantalica* Piton | Joursac, France | Piton and Theobald, 1935 |
| *Lasius crispus* Piton | Joursac, France | Piton and Theobald, 1935 |
| *Lasius martynovi* Popov | Caucasus, U.S.S.R. | Popov, 1933 |
| *Oecophylla leakeyi* Wilson and Taylor | Kenya | Wilson and Taylor, 1964 |

*Extinct genera.

is so highly polyphyletic remains unanswered, and is a problem unlikely to be resolved by the geological past.

However, the fossil record does provide intriguing information on the evolution of the bees and indicates that their sociality may well have been established prior to the Oligocene. The following survey of the fossil Apoidea is indicative of the diversity of bees which have been found (Table 5). Those species which were described by early 19th century entomologists (Latreille, Heer, Heyden, etc.) are excluded from this coverage because these were uniformly assigned to modern genera.[8] Cockerell (1909) claims that most of these species actually belonged to quite different and extinct genera.

*Oligocene*

The earliest bees in the fossil record are found in the Baltic Amber, of Lower Oligocene age. The bees in this deposit are well-diversified (Zeuner and Manning, 1976), and the most prevalent apoid genus in the amber, *Electrapis,* is thought to have been social. Cockerell (1909) based this conclusion on the occurrence of many specimens of *Electrapis meliponoides* crowded together in a small piece of amber, a suggestive but certainly not conclusive deduction. Zeuner (1944, 1951), however, believed *Electrapis* to be social based on its pollen collecting apparatus. The extent to which social behavior was developed in this genus nevertheless remains a matter of conjecture. *Electrapis* is considered by some to be directly ancestral to the highly eusocial *Apis,* although Kelner-Pillault (1974) disagrees with this relationship. She suggests that *Electrapis* is actually a long extinct genus which possessed many primitive characters and represents an evolutionary side-line of the Apoidea. Both hypotheses are highly conjectural.

The presence of long-tongued bees such as *Electrapis* suggests that the Baltic Amber bees were rather specialized. Tongue structure is assumed to have evolved in response to various morphological changes (i.e., longer corollas) which took place during the evolution of the angiosperms (Michener, 1974). Short-tongued bees such as the colletids are considered the more primitive members of the Apoidea and are representative of bee radiation that occurred at a time when most of the angiosperms had shallow flowers (Michener, 1974).

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[8]For a listing of these specimens, see Zeuner and Manning (1976).

In Late Oligocene deposits, the Apoidea are extremely well represented. Six major families of bees are known from this epoch: Halictidae, Andrenidae, Melittidae, Megachilidae, Anthophoridae, and Apidae. A total of 29 genera are represented, many of which are extant. Several specimens belonging to *Chalcobombus* and *Bombus* are described from deposits in both Europe and North America suggesting widespread radiation of this specialized group of bees by the Early Oligocene. In the Late Oligocene, bees very similar to *Apis mellifera* are found. Manning (1952) feels that some species from the Rott Shales possess almost all the necessary characters for placement in the genus *Apis* (Fig. 4). Moreover, in the Dominican Amber of Oligocene-Miocene age, several *Trigona* workers are found, providing convincing proof that social behavior was well established at this time (Michener, 1974).
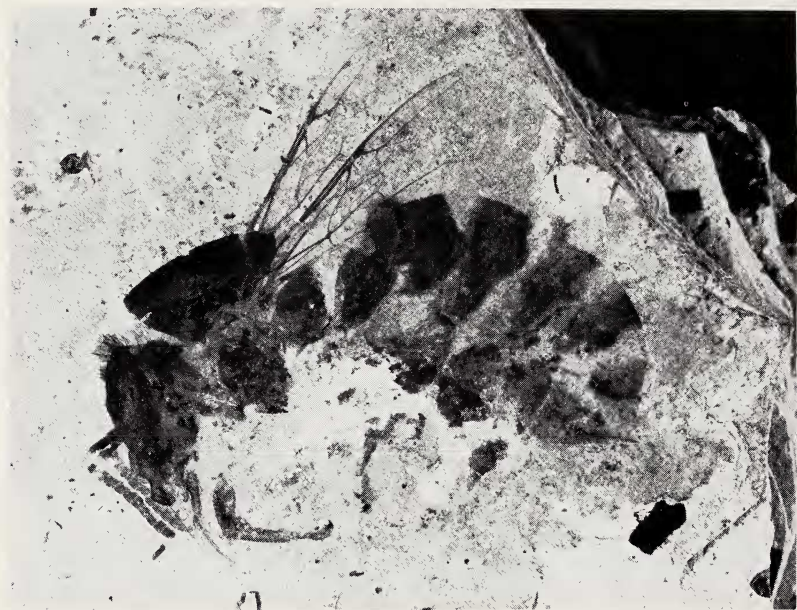


Figure 4. *Apis henshawi* Cockerell from Upper Oligocene of Rott, Germany. Original photograph of holotype in Museum of Comparative Zoology. Length of body, 15 mm.

*Miocene*

By the Miocene, the bee fauna is essentially modern. In Chiapas Amber from Mexico, bees have been discovered that are so similar to an existing Neotropical species that they have been assigned to the same subgenus, *Trigona* (*Nogueirapis*), and are scarcely different at the specific level (Wille, 1959). Fujiyama (1970) mentions the discovery of a fossil bee in a Japanese Miocene deposit and states that, "There is no room for doubt that this is a species of honeybee."

A review of the fossil record reveals the following about the evolution of the bees. 1) We know that the Early Oligocene fauna is a mixture of primitive and advanced genera, although it appears to be dominated by fairly advanced species. By the end of this epoch, the fauna is modern in overall character. 2) We know that sociality had clearly arisen by the end of the Oligocene, and possibly much earlier. And 3) by the Miocene, the bees were virtually indistinguishable from the bees of today. Six families of bees are represented in the Oligocene: including the phylogenetically advanced Apidae with six genera and 22 species. Such diversity of relatively advanced bees is indicative of either a much longer history of the group than is evidenced by the fossil record, or a fairly short history characterized by the rapid speciation and explosive radiation of the group.

The bees are clearly derived from the spheciform wasps, although nothing is known about the nature of this sphecid ancestor (Wilson, 1971; Michener, 1974). In 1964, just prior to his death, F. J. Manning was investigating a sphecid from the Jurassic beds of Lerida Province, Spain, which "he thought might be (or be closely related to) the ancestor of the bees" (Zeuner and Manning, 1976, p. 155). This would be an astounding find if true, and it is unfortunate that nothing more is known — either about the specimen or about Manning's reasons for thinking it ancestral to the bees.

The distinction between the Sphecoidea and the Apoidea is sufficiently subtle as to make determinations of fossil compressions extremely difficult. The presence of plumose hairs and enlarged basitarsi, characters which are important apoid features, rarely survive preservation unless the insect is preserved in amber.

The origin of the bees remains a subject of much speculation. It is believed that "insect-plant interactions played a key role in the origin of the angiosperm flower and component structures" (Hickey

and Doyle, 1977, p. 92). Conversely, angiosperms have been instrumental to the evolutionary success of the Apoidea. On the basis of the evolutionary dependence of the two groups, can anything be said about their relationship in geological time? Two possibilities present themselves: 1) the angiosperms evolved first and were initially wind pollinated[9] or pollinated by arthropods other than Hymenoptera (e.g., Coleoptera, Diptera, Thysanoptera, possibly spiders); and 2) the first bees evolved from sphecid wasps prior to the origin of the angiosperms by adapting themselves to feeding on pteridosperm pollen or reproductive organs.

A closer look at these possibilities is warranted. Coleoptera and Diptera are found in the fossil record at least by the Triassic. This supports the argument that they could have served as vectors for dispersal of angiosperm pollen. The question arises, if these insects were capable of performing essential roles as pollinators, why didn't angiosperms arise earlier in the Mesozoic than the Cretaceous? Regal (1977) suggests that the limiting factor to angiosperm dispersal was the presence of seed-carrying birds and mammals. He argues that this method of seed dispersal, acting in conjunction with insect pollination, provided the selective advantages behind the subsequent primary radiation of the angiosperms. This is a sound argument, but says little about the insects which may have been pollinating these early plants. It would seem that successful dispersal of flowering plants is dependent on efficiency at two levels — pollination and seed dispersal. The explosive radiation of the angiosperms during the Cretaceous indicates that the more specialized insect pollinators, the bees, may have been present in order to explain this success.

This might support the possibility that pollen collecting bees had already evolved by the time the first angiosperms appeared. According to Wilson (1971, p. 75), the "Apoidea can be loosely characterized as sphecoid wasps that have specialized in collecting pollen instead of insect prey as larval food." The possibility, however speculative, exists that bees evolved in response to the food source presented by the pteridosperms but subsequently abandoned this resource when the angiosperms appeared. Certainly one way of accounting for the explosive radiation of the angiosperms would be

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[9]Stebbins (1970, p. 323) suggests that the earliest angiosperms were not wind pollinated.

TABLE 5.   APOIDEA IN THE FOSSIL RECORD.[10]

| Geological Age | Locality |
|---|---|
| **EOCENE** | |
| ?Apidae | |
| *Probombus hirsutus* Piton | Menat, France |
| **OLIGOCENE** | |
| Halictidae | |
| *\*Cyrtapis anomalis* Cockerell | Florissant, Colorado |
| *Halictus ruissatelensis* Timon-David | Marseille, France |
| *Halictus florissantellus* Cockerell | Florissant, Colorado |
| *Halictus miocenicus* Cockerell | Florissant, Colorado |
| *Halictus scudderiellus* Cockerell | Florissant, Colorado |
| Andrenidae | |
| *Andrena wrisleyi* Salt | Baltic Amber |
| *Andrena clavula* Cockerell | Florissant, Colorado |
| *Andrena grandipes* Cockerell | Florissant, Colorado |
| *Andrena hypolitha* Cockerell | Florissant, Colorado |
| *Andrena lagopus* Latreille | Florissant, Colorado |
| *Andrena percontusa* Cockerell | Florissant, Colorado |
| *Andrena sepulta* Cockerell | Florissant, Colorado |
| *\*Lithandrena saxorum* Cockerell | Florissant, Colorado |
| *\*Pelandrena reducta* Cockerell | Florissant, Colorado |
| *\*Libellulapis antiquorum* Cockrell | Florissant, Colorado |
| *\*Libellulapis wilmattae* Cockerell | Florissant, Colorado |
| Melittidae | |
| *\*Ctenoplectrella dentata* Salt | Baltic Amber |
| *\*Ctenoplectrella viridiceps* Cockerell | Baltic Amber |
| *\*Ctenoplectrella splendens* Kelner-Pillault | Baltic Amber |
| *\*Glyptapis fuscula* Cockerell | Baltic Amber |
| *\*Glyptapis mirabilis* Cockerell | Baltic Amber |
| *\*Glyptapis neglecta* Salt | Baltic Amber |
| *\*Glyptapis reducta* Cockerell | Baltic Amber |
| *\*Glyptapis reticulata* Cockerell | Baltic Amber |
| *Melitta willardi* Cockerell | Baltic Amber |
| Megachilidae | |
| *Anthidium mortuum* (Meunier) | Rott, Germany |
| *Anthidium exhumatum* Cockerell | Florissant, Colorado |
| *Anthidium scudderi* Cockerell | Florissant, Colorado |
| *\*Dianthidium tertiarium* Cockerell | Florissant, Colorado |
| *\*Lithanthidium pertriste* Cockerell | Florissant, Colorado |
| *Heriades bowditchi* Cockerell | Florissant, Colorado |
| *Heriades halictinus* Cockerell | Florissant, Colorado |
| *Heriades laminarum* Cockerell | Florissant, Colorado |
| *Heriades mersatus* Cockerell | Florissant, Colorado |

[10]See Zeuner and Manning (1976) for reference citations.